

Appearance of Ossification Centers of the Lower Arm, Wrist, Lower Leg, and Ankle in Immature Orangutans and Chimpanzees With an Assessment of the Relationship of Ossification to Dental Development

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ABSTRACT This study examines the appearance of the secondary ossification centers in the lower arms, wrists, lower legs, and ankles of a cross-sectional sample of 20 infant orangutans and chimpanzees (15 of known age). The number of tarsal and carpal centers is analyzed relative to the degree of M_1 development and the weight of individual animals. Variation in the appearance of these ossification centers is discussed relative to these variables and others. In addition, a sequence of appearance is established for the carpal and tarsal ossification centers in the orangutan and data is presented on the status of these centers in a fetal and newborn gorilla. Study results indicate that 1) there is variation in the number of secondary epiphyses present in animals of similar ages; 2) tarsal ossification is completed prior to carpal ossification in the orangutan; 3) there are indications of a relationship between weight and the number of ossification centers present in animals of similar age; and 4) there appears to be no evidence of specific relationships between carpal and tarsal development and M_1 development. © 1996 Wiley-Liss, Inc.

Recent analyses of primate life history (Harvey and Clutton-Brock, 1985; Harvey et al., 1986; Siebert et al., 1984; Smith, 1989a,b, 1991, 1993) have used numerous somatic growth measures, including gestation length, the patterns and ages of dental eruption, various measures of sexual maturity (age of menarche, age of first breeding, the presence of secondary sexual characteristics), and comparisons of postnatal growth periods. Such life history data provide insights into variability within and similarities and differences between primate taxa. In addition, they provide a basis for hypothesizing about the life history of extinct primates and the evolutionary relationships of extant and fossil primates.

In addition to reconstructing primate life history, life history information is critical in establishing somatic growth norms in order

to assess the development of living primates (in both captivity and the wild). However, since the chronology of somatic development may vary from one morphological system to another (Demirjian, 1986; Harvey and Clutton-Brock, 1985; Schultz, 1956; Smith, 1991, 1993; Swindler, 1985; Watts, 1985, 1990), comparative studies of intra- and interspecific primate growth are often limited to data from a single somatic system or to a single measure of physiological growth, e.g., the teeth, the appearance of secondary ossification centers, menarche, etc. (see references in previous paragraph). For many primates, including the great apes (with the exception of the common chimpanzee [*Pan troglodytes*] which has merited several studies), informa-

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tion is still inadequate to establish the parameters of postnatal development for even a single system.

In contrast, numerous studies have been published on humans (Demirjian, 1986; Fanning, 1961; Garn et al., 1965a,b, 1967; Greulich and Pyle, 1959; Lewis and Garn, 1960; Moorrees et al., 1963; Pyle and Sontag, 1943; Roche, 1992) which have established norms for the growth of European-derived populations, including development of the teeth and skeleton. Other studies (Alvarez and Navias, 1989; Garn et al., 1965a,b, 1966a,b, 1967; Roche, 1992) have examined height, weight, and various environmental influences (diet, race, etc.) on human growth, demonstrating developmental differences in the skeleton as a result of malnutrition, ethnic affinity, and sex. There is also evidence of sex differences in tooth development and some evidence of delayed tooth development as a result of malnutrition (Alvarez and Navias, 1989; Garn and Rohmann, 1966), although the teeth appear to be more resistant to environmental insults such as malnutrition (Garn et al., 1965a,b; Lewis and Garn, 1960).

Using the available normative data, many of these studies also assessed potential relationships between the development of the various morphological systems in humans (see Roche, 1992, for review), including the skeleton and teeth. Specific attempts to correlate the events of human dental development with skeletal development (Alvarez and Navias, 1989; Garn et al., 1965b; Liliequist and Lundberg, 1971) have demonstrated some general similarities in the relative chronology in which each system develops (children with accelerated skeletal development tend also to accelerate some parameters of dental development). Nevertheless, attempts to relate specific events of dental development (completion of the deciduous dentition, eruption of M_1^I , etc.) with the development of the skeletal system (appearance of secondary ossification centers, etc.) have found few direct associations and relatively low correlations prior to the onset of adolescence (Lewis and Garn, 1960).

As mentioned above, compared to the wealth of information on European-derived human populations, knowledge of the pa-

rameters of anthropoid development, particularly that of the great apes, is limited and largely derived from cross-sectional studies of zoo or museum specimens or from longitudinal studies of captive-reared animals (Anemone et al., 1991, 1993; Conroy and Mahoney, 1991; Dean and Wood, 1981; Gavan, 1953; Krogman, 1930; Kuykendall, 1992; Kuykendall and Conroy, 1993; Marzke et al., 1993; Newell-Morris et al., 1980; Nissen and Riesen, 1949a,b; Schultz, 1936, 1940, 1941, 1956; Sirianni and Swindler, 1985; Tarrant and Swindler, 1972; Watts, 1990). The most comprehensive studies of wild apes have been those of Schultz (1940, 1941) and provide some of the most complete information available on the general growth and development of the chimpanzee and the orangutan including the skeleton and teeth (based on cross-sectional samples). However, despite Schultz's large samples, the lack of specimens in some age categories limits discernment of many details of skeletal or dental development. Longitudinal studies of relatively small samples of captive-reared chimpanzees such as those of Nissen and Riesen (1945; 1949a,b) have provided information on teeth eruption, the appearance of postnatal secondary ossification centers, and the relationship of ossification to environmental factors. More recently, a number of studies have provided further information on dental development in one or more of the great apes (Anemone et al., 1991, 1993; Dean and Wood, 1981; Kuykendall, 1992; Kuykendall et al., 1993; Swindler, 1985; Winkler et al., 1991, 1994).

Although these studies provide valuable data needed in the assessment of primate growth patterns, much remains unknown. As was mentioned above, several recent studies have focused on dental development, but little has been done, other than the work of Nissen and Riesen (1949a, b), to document the appearance of secondary ossification centers or to assess variation in the sequence of their appearance. As was noted by Nissen and Riesen (1949a) over 40 years ago, such data continue to be extremely meager. In order to begin to fill this void, the present study has been undertaken for the purpose of establishing the sequential appearance of the secondary ossification centers of the

TABLE 1. The appearance of the secondary epiphyses in immature orangutans (*Pongo pygmaeus*)

Orangutans	Dental status ²	Sex ³	Distal epiphysis of ulna ¹	Distal epiphysis of radius ¹	Capitulum of radius ¹	Distal epiphysis of tibia ¹	Prox. epiphysis of tibia ¹	Distal epiphysis of fibula ¹	Number of carpals	Number of tarsals
Newborn	N	M	—	P	?	—	?	—	2	2
18-day-old	N	F	—	—	—	—	—	—	2	4
2-month-old	N	F	—	—	?	—	—	—	2	4
9-month-old	P	F	—	P	?	P	?	P	3	6
Unknown age	P	M	P	P	?	?	P	?	4	6
12-month-old	D	F	P	P	P	P	P	P	5	7
Unknown age	D	F	P	P	?	P	P	?	7	6
16-month-old	D	F	P	P	?	P	P	P	7	7
17-month-old	D	F	P	P	P	P	P	P	8	7
4-year-old	M	M	P	P	P	P	P	P	7	7

¹ P = present.² Dental status = N: no teeth in occlusion, P: partial deciduous, D: full deciduous, M: M1 emerging or in occlusion.³ M = male, F = female.

wrist, lower arm, lower leg, and ankle of the orangutan, examining their presence in a sample of immature chimpanzees, and assessing possible associations between carpal and tarsal development and tooth development in these animals. In addition, information is provided on the state of development of these secondary ossification centers in a newborn and fetal gorilla. Previous information on skeletal development in the gorilla has been limited to data presented by Schultz (1956, 1968) on ossification centers in a neonate and a study of ossification and epiphyseal fusion in an older sample which included no neonates (Randall, 1944).

MATERIALS AND METHODS

One of the goals of this study was to limit the sample as much as possible to either wild-caught or mother-reared (in captivity) animals which were not subject to manipulation or experimentation. Therefore, due to the impossibility of implementing longitudinal radiographic studies in the wild on infants and the inadvisability of removing infants from their mothers in captive settings, the sample was by necessity cross-sectional. The sample includes 9 infant orangutans and a 4-year-old, 9 of which were mother-reared during infancy (the 12-month-old was nursery-reared). Two of these were wild-captured and of unknown age. The remaining orangutans are of known age (see Table 1 for details of sex, age, dental eruption status, etc.). The 2 orangutans for which no chronological age was available are part of the

Adolph Schultz collection of the Anthropological Institute of the University of Zürich. The sample also included 10 chimpanzees (*Pan troglodytes*), 7 of known age, which were obtained from Yerkes Regional Primate Center (see Table 2 for details of sex, age, dental eruption status, etc.) The unknown age chimpanzees were from the collections of the Anthropological Institute of the University of Zürich. Two of these were wild-captured and the background of the remaining unknown age chimpanzee was unknown. All animals reared in captivity died of natural causes, most from illnesses of brief duration. The newborns (see Table 1 and 2) were all stillbirths. The first 2 chimpanzees listed in Table 2 were twins. With the exception of the third newborn chimpanzee listed in Table 2, all neonates had recorded weights within the published norms (Fooden and Izor, 1983; Nissen and Riesen, 1949a; Schultz, 1973). The weight of this exception (wt. = 1.27 kg.) was in the lower end of published ranges (Fooden and Izor, 1983; Nissen and Riesen, 1949a; Schultz, 1973). In order to determine whether the low weight specimen had a full-term gestation and was therefore of the same chronological age as the remaining newborns, the M₁ was dissected from it and examined for commencement of calcification. Since calcification had commenced on this tooth and M₁ begins to calcify very late in gestation, generally in the last month of a full-term pregnancy (Dean and Wood, 1981; Oka and Kraus, 1969; Swindler, 1985; Tarrant and Swindler, 1972; Winkler

TABLE 2. The appearance of the secondary epiphyses in immature chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*)

	Dental status ²	Sex ³	Distal epiphysis of ulna ¹	Distal epiphysis of radius ¹	Capitulum of radius ¹	Distal epiphysis of tibia ¹	Prox. epiphysis of tibia ¹	Distal epiphysis of fibula ¹	Number of carpals	Number of tarsals
Chimpanzees										
Newborn	N	F	—	?	—	—	—	—	2	2
Newborn	N	M	—	—	—	—	—	—	1	2
Newborn	N	F	—	P	?	—	?	—	1	2
Newborn	N	M	—	P	—	P	P	P	2	5
Newborn	N	F	—	P	—	—	?	—	2	4
Newborn	N	M	—	—	—	—	—	—	2	4
Unknown age	D	M	?	P	P	P	P	P	3	5
19 month old	D	F	?	P	P	P	P	P	5	5
Unknown age	D	F	P	?	P	P	P	P	6	6
Unknown age	M	F	P	P	P	?	P	?	8	7
Gorillas										
Fetus	N	F	—	—	—	—	—	—	0	2
3-day-old	N	?	—	P	P	—	P	—	2	4

¹ P = present.² Dental status = N: no teeth in occlusion, P: partial deciduous, D: full deciduous, M: M1 emerging or in occlusion.³ M = male, F = female.

et al., 1991; Winkler, in press), this low birth weight animal did not appear to be markedly premature.

The crania of all specimens were radiographed in lateral aspect in order to reveal details of dental development using methodology described in other papers (Winkler et al., 1991, 1994, 1996). Stages of crown and root development and alveolar emergence or eruption (defined as movement of the tooth above the alveolar plane) were recorded for all teeth. Both right and left lower arms, wrists, lower legs, and ankles of each specimen were radiographed in standard A-P position and all were analyzed for the appearance of secondary ossification centers. A center was recorded as ossified if any part of it appeared ossified from its initial appearance as a white dot. Data was recorded on the number, relative size (an indicator of how recently it had ossified), and type of carpal and tarsal ossification centers present. For the sake of accurate identification and verification of carpal and tarsal position, all wrist and ankle radiographs were compared with radiographs of these regions of a juvenile chimpanzee and orangutan which possessed all the secondary ossification centers, and with the bony skeletons of adult animals.

The orangutan possesses a separate os centrale postnatally in its wrist; therefore, 9 secondary ossification centers are present (compared to the 8 centers present in hu-

mans and the other great apes). The os centrale generally fuses with the scaphoid (navicular) prenatally or shortly after birth in the other great apes and humans (Schultz, 1936, 1941). Schultz (1941) reports that this fusion between the scaphoid and os centrale may occur in some adult orangutans.

For each specimen, the appearance of the secondary ossification centers was compared with M₁ development. M₁ was chosen for these comparisons since its development encompassed the age span represented in the sample, just beginning development in the youngest and fully erupted and undergoing root development in the oldest specimens. In order to assess variability on carpal and tarsal ossification relative to tooth development, the number of carpal and tarsal centers present was graphed relative to the stages of M₁ crown development of each specimen. In addition, in order to explore possible relationships between the weight of individual animals and skeletal ossification, the number of carpal and tarsal centers ossified was graphed relative to the weight of specimens for which weights were available ($n = 14$).

Although other studies on apes and humans have demonstrated differences between the sexes in aspects of skeletal development, and to a lesser degree, dental development (Fooden and Izor, 1983; Garn et al., 1967; Lewis and Garn, 1960; Marzke

TABLE 3. Associations between the appearance of chimpanzee/orangutan ossification centers and dental eruption

	No. teeth	Partial deciduous	All deciduous	M ₂ erupted
Carpals	1-2/2-3	?/3-5	3-7/5-8	8/7-9
Tarsals	2-5/2-4	5/6	5-6/6-7	7/7

et al., 1996; Nissen and Riesen, 1949a; Pyle and Sontag, 1943), the numbers for each sex of each taxon in this sample are too small to examine differences between the sexes. For instance, there are only 3 male orangutans in the entire sample. Therefore, although variation will be discussed in the combined sample, no attempt has been made in this paper to specifically compare males and females.

RESULTS

General relationships

Tables 1, 2, and 3 provide information on general relationships between the status of tooth eruption and the number of secondary ossification centers present in the study specimens. Even with this small sample, there is fairly marked variation in the number of tarsals, carpals, and in the other secondary epiphyses in 2 specimens of similar eruption status or age. This range at birth can be demonstrated by a comparison of the tarsal region of a newborn female chimpanzee which has only 2 ossification centers present (see Fig. 1) with the tarsus of a newborn male chimpanzee with 5 ossification centers visible (see Fig. 2). There is less difference between the chimpanzees in Figures 1 and 2 in the number of carpal ossification centers. The female of Fig. 1 has only 1 carpal center visible in its wrist (not shown in figure), whereas the wrist of the male has 2 carpal centers (see Fig. 2).

The neonates here (of all 3 genera) demonstrate greater variability than indicated by previous studies (Schultz, 1956, 1968; cited by Schwartz, 1987) (see Tables 1 and 2). For example, the newborn orangutan in this study possesses a distal epiphysis of the radius (contra Schultz 1956, 1968). However, it should be noted that 2 older orangutans in this study did not yet possess this epiphysis (see Table 1). In addition, there is greater

variability in tarsal and carpal number in the neonatal chimpanzees here (see Table 2) than indicated by Schultz (1956, 1968). And, whereas Schultz (1968) indicates (in a figure) the presence of only 1 carpal and the distal epiphysis of the radius in a neonatal gorilla, the 3-day-old gorilla of this study (see Table 2) has 2 carpals and 3 other secondary epiphyses.

The appearance of the tarsal secondary ossification centers seems to be more rapid than that of the carpal centers. Six tarsal ossification centers are present in the ankle of the 9-month-old orangutan (see Fig. 3) in which only 3 carpal centers have ossified. All 7 tarsal ossification centers and other secondary epiphyses examined are visible in a radiograph of the 12-month-old orangutan (which is completing its deciduous dentition) (see Fig. 4), whereas only 5 carpal centers are present (see Table 1). In a similar fashion, all tarsal and other secondary epiphyses examined have ossified in both the 16-month-old orangutan, which has 7 carpal elements present (see Fig. 6) and the 17-month-old orangutan which has 8 carpal elements present (see Fig. 5). In contrast, one of the unknown age orangutans which has tooth development intermediate between the 12-month-old and 16-month-old orangutans (see Table 1) has 7 carpal centers and only 6 tarsal centers present.

Overall, the development of the specimens in this study suggests that the secondary ossification centers of lower arm and leg and the tarsus generally complete their appearance during the second or third year of life in this hominoid, after the eruption of the deciduous dentition but prior to the appearance of M₂. Completion of carpal ossification appears slightly later but within the same general time period. Schultz (1941) indicates that in the orangutan, generally most or all the tarsal and carpal centers are present during the developmental period in which the deciduous teeth are in occlusion, but no permanent teeth have yet erupted. Schultz (1941) also demonstrates variability in the presence of some of the secondary epiphyses (proximal epiphysis of the radius and distal epiphysis of the ulna) during this developmental period. He further reports that ossification centers are present for all the second-

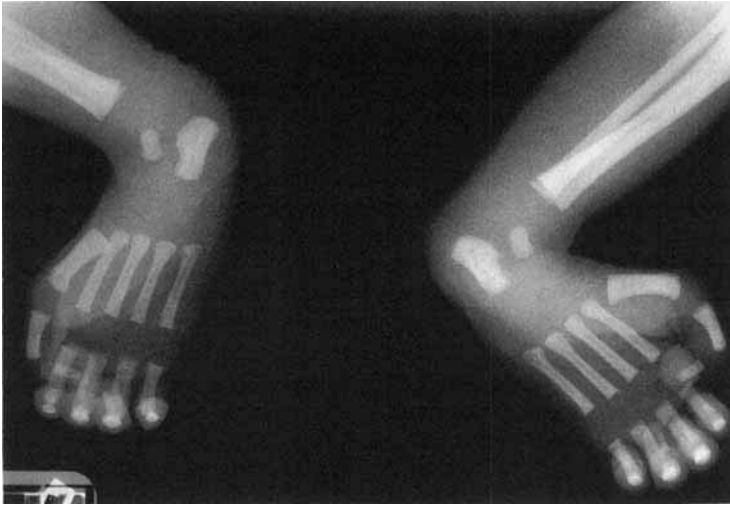


Fig. 1. Radiograph of the ankles of a newborn female chimpanzee (Table 2, #3) with secondary centers present for calcaneus and talus.



Fig. 2. Radiographs of the wrists (**top**) and ankles (**bottom**) of a male newborn chimpanzee (Table 2, #6). Note that there are two carpals and five tarsals present.

ary epiphyses of the limbs by the time of M_1^I alveolar emergence.

Very little can be said about the timing of the appearance of the secondary ossification centers in the chimpanzee due to the limited sample of anything but neonates. However, tarsal ossification is not yet complete in any of the chimpanzee specimens which have fully erupted deciduous dentition. The only chimpanzee which demonstrates the presence of all 7 tarsal ossification centers is the last one listed in Table 2, which has an erupted M_1^I (M_1^I erupt during the third or fourth years of life in the chimpanzee [Anemone et al., 1991; Dean and Wood, 1981; Nissen and Riesen, 1964]) and therefore is of an older chronological age. All 7 tarsal centers were visible by the end of the third year of life in the laboratory reared chimpanzees studied by Nissen and Riesen (1949a). As in the orangutan, the carpals of the chimpanzee are also completed prior to or around the time of M_1^I emergence. All other lower leg and arm secondary epiphyses which could be examined are present in the chimpanzees of this study which had full deciduous dentitions. However, the work of Schultz (1956) indicates some variability during this developmental stage in the presence of the distal epiphyses of the ulna and fibula.

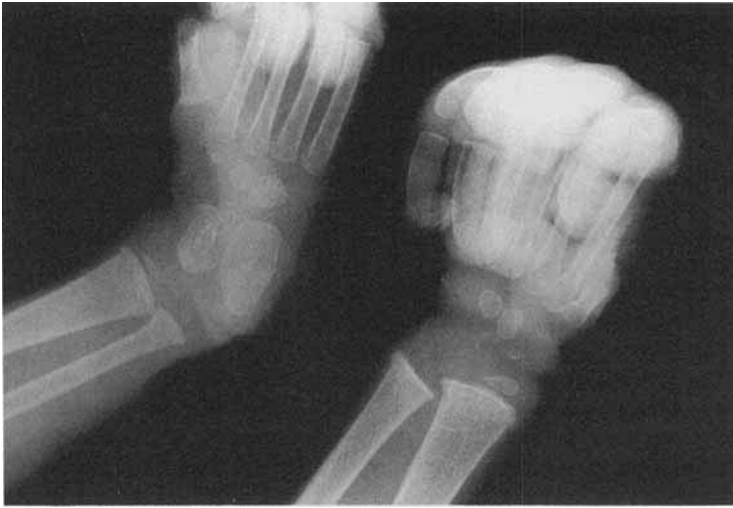


Fig. 3. Radiograph of the wrist (**top**) and ankle (**bottom**) of the 9-month-old female orangutan (Table 1, #4).



Fig. 4. Radiograph of the ankle of the 12-month-old female orangutan (Table 1, #6). Note that all 7 tarsal bones are present.

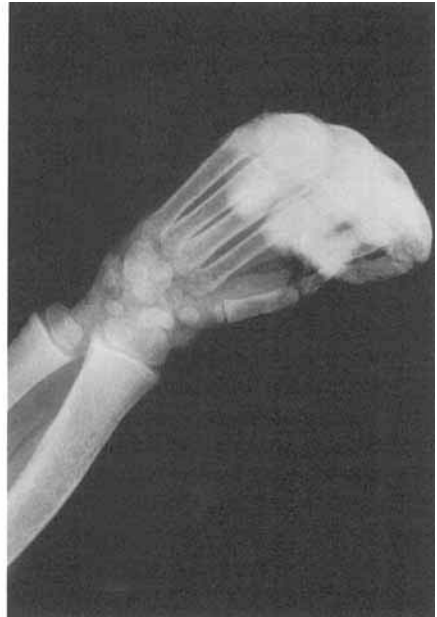


Fig. 5. Radiograph of the wrist of the 17-month-old female orangutan (Table 1, #9).

Comparisons with M_1 development

Figures 7 and 8 demonstrate the relationship in each specimen between M_1 develop-

ment and the number of tarsal and carpal ossification centers present. The variability in numbers of carpals and tarsals at any particular stage of M_1 is so large that only



Fig. 6. Radiograph of the wrist (**right**) and ankle (**left**) of the 16-month-old female orangutan (Table 1, #8).

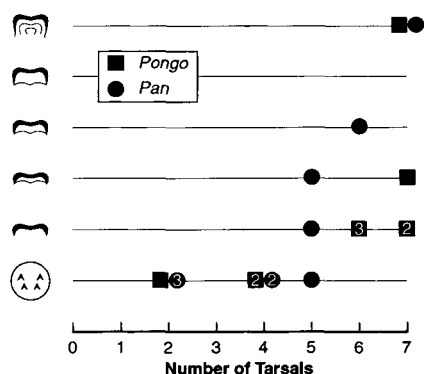


Fig. 7. The relationship of tarsal development to M_1 development.

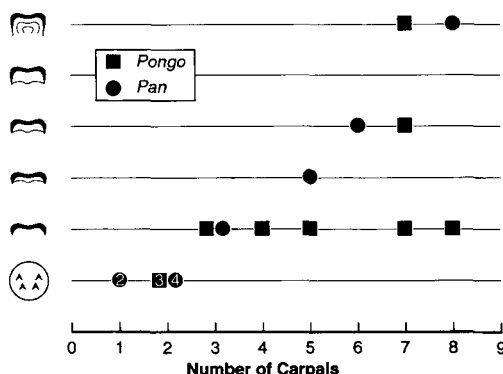


Fig. 8. The relationship of carpal development to M_1 development.

very general associations can be made. For instance, although specimens in which M_1 is further developed tend to have greater numbers of tarsal or carpal centers present, there are exceptions, such as the orangutan specimen in Figure 8, which has 8 carpals ossified, but the crown of its M_1 is only approximately $\frac{1}{4}$ complete.

Comparisons with weight

Figures 9 and 10 demonstrate the relationship between the weight of each specimen and the number of tarsal and carpal

centers present. There seems to be more evidence for a possible relationship between weight and number of secondary ossification centers than there was for tooth development. For instance, the heaviest neonatal chimpanzee (Table 2, fourth on the list) has the highest number of tarsal centers (see Figs. 9 and 2). The same pattern is also evident for carpal ossification where the heavier neonates have 2 carpals present, but the lower weight specimens only have 1 (see Fig. 10). However, the limited number of specimens and the variability in both weight and

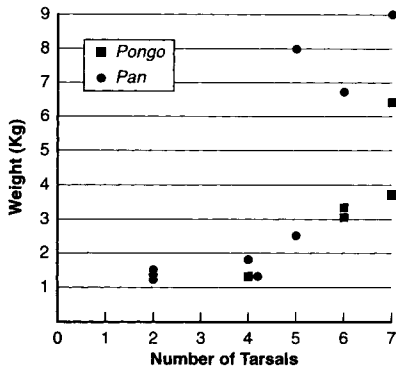


Fig. 9. The relationship of tarsal development to weight.

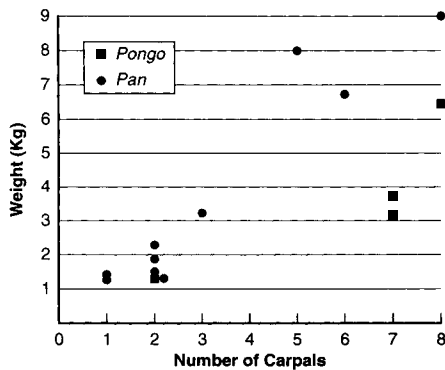


Fig. 10. The relationship of carpal development to weight.

number of ossification centers make it difficult to clearly define such a relationship in the older specimens studied here.

Sequence of appearance of ossification centers

A partial sequence of carpal ossification in the orangutan based on the results of this study combined with data presented by Schultz (1941) is provided in Table 4. The capitate and hamate generally appear prenatally (Schultz, 1941) and are present in both neonatal orangutans in the sample. The remaining centers appear in the listed order (Table 4) in specimens of sequential age. The sequence for the appearance of os centrale and trapezoid could not be determined.

This is the first time that a partial se-

TABLE 4. A comparison of the order of carpal ossification¹

Chimpanzee	Orangutan	Human
Capitate	Capitate	Capitate
Hamate	Hamate	Hamate
Triquetral	Scaphoid	Triquetral
Trapezium	Trapezium	Lunate
Lunate	Lunate	Trapezium
Scaphoid	[Trapezoid]	Scaphoid
Pisiform	[Os centrale]	Trapezoid
Trapezoid	Triquetral	Pisiform
	Pisiform	

¹Sequence of ossification for chimpanzee and orangutan partially based on present study combined with data from Schultz (1941) and Nissen and Riesen (1949a). Human sequence from Pyle and Sontag (1943).

quence of carpal ossification has been established for the orangutan and, as indicated in Table 4, it differs from the most common sequences of ossification in humans (Garn et al., 1966a, 1967; Pyle and Sontag, 1943) and from that seen here and published elsewhere for the chimpanzee (Nissen and Riesen, 1949a). However, variation in the sequence of appearance of carpal ossification centers is quite common in humans (Garn et al., 1967; Pyle and Sontag, 1943; Roche, 1992) and there is considerable overlap in the age of appearance of the carpal ossification centers in the chimpanzee (Nissen and Riesen, 1949a). Considerable variability in the sequence of appearance of the carpals at birth has also been reported in macaques (Emel and Swindler, 1990). Therefore, such variation will most likely be revealed in further studies of the orangutan. However, despite the likelihood of variability in the overall carpal ossification sequence, the capitate and hamate are reported to be the initial carpal centers to appear in other primates (Newell-Morris and Tarrant, 1978).

Contrary to the evidence above suggesting possible differences between the hominoids in the sequence of carpal appearance, the sequence of appearance of the tarsal ossification centers appears to be the same in both the chimpanzee and orangutan (in sequence: calcaneus, talus, cuboid, lateral cuneiform, medial cuneiform, intermediate cuneiform, navicular) (based in part on data from Nissen and Riesen, 1949a; Schultz, 1941). This sequence is also similar to that commonly seen in humans (Garn et al., 1966, 1967; Pyle and Sontag, 1943), although Garn et

al. (1966) have documented several variations in this sequence. The calcaneus and talus appear prenatally in all these hominoids. Schultz (1941) reported that the talus appears shortly before birth. However, both centers are present in an orangutan fetus of approximately 6 months gestation age (AS 1647, age estimate from Schultz, 1941).

DISCUSSION

The results of this study are comparable to those of earlier studies (Cheverud, 1981; Glassman, 1983; Lewis and Garn, 1960; Nissen and Riesen, 1949a), which found limited correlations between dental development and skeletal development in humans and other primates and no evidence of specific relationships between events of dental development and the onset of ossification in chimpanzees. However, a comparison of the number of centers present relative to each specimen's weight (see Figs. 9 and 10) may provide some support for a correlation with weight when age is held constant (see discussion above). Unfortunately, the sample size is too small in this study to examine this relationship statistically. However, studies on humans (Garn et al., 1965b, Garn and Rohmann, 1966) have found that heavier children are ahead of their leaner peers in osseous development. Similarly, earlier studies on chimpanzees (Nissen and Riesen, 1949a) have found some correlation between mean ossification rate and birth weight.

Other factors such as the sex of an individual or whether an individual is bottle or mother-fed may also be related to the relative rate of postnatal ossification. Data from humans, chimpanzees, and several other primate species (Cheverud, 1981; Galliari, 1988; Garn et al., 1967; Greulich and Pyle, 1959; Hayama, 1965; Marzke et al., this volume; Newell-Morris and Tarrant, 1978; Nissen and Riesen, 1949a; Pyle and Sontag, 1943; Roche, 1992; Sirianni and Swindler, 1985; Sontag et al., 1939; Wagenen and Asling, 1958) indicate that females are skeletally advanced relative to males of the same age in terms of the number, size, and timing of ossification centers and in their fusion. Studies by Watts (1985, 1990) comparing a number of primates have also indicated that

females are skeletally advanced for both gestation time and birth weight when compared to males. Other studies on macaque species (Cheverud, 1981; Hayama, 1965; Wagenen and Asling, 1958) have demonstrated earlier epiphyseal fusion in females than in males. Nevertheless, in contrast to the above studies, other studies on several species of African and New World monkeys (Tappan and Severson, 1971; Wintheiser et al., 1977) failed to find significant differences between the sexes in the timing of epiphyseal fusion.

Studies on chimpanzees have also indicated that the appearance of ossification centers in mother-reared infants is delayed relative to nursery or bottle-reared infants (Marzke et al., 1996; Nissen and Riesen, 1949b). The weight gain of bottled-reared chimpanzees is substantially greater than those of the mother-reared (Marzke et al., 1996; Nissen and Riesen, 1945) and may be a factor to consider in the differences reported in osseous development.

As mentioned above, all 7 tarsal ossification centers appear to be present in the orangutan by the time of M_1 eruption and all carpal centers are present shortly thereafter. Evidence from the chimpanzees studied here indicates that tarsal development is also completed before or around the time of M_1 eruption with carpal development again being completed shortly thereafter. These developmental time frames are similar to those previously reported by Schultz (1940, 1941, 1956) and Nissen and Riesen (1949a).

Previous studies demonstrated that orangutans grow more slowly than chimpanzees (Brandes, 1939) and that epiphyseal union in the orangutan is slightly later than in the chimpanzee (Schultz, 1941). For instance, many epiphyses were unfused at the time of dental eruption completion in both apes, but many more had fused in the chimpanzee than in the orangutan (Schultz, 1956). However, based on this infant sample, there is no evidence of slower growth in the orangutan. On the contrary, it appears that tarsal development is somewhat slower in the chimpanzee than in the orangutan. As discussed above, the only chimpanzee specimen with all 7 tarsals present has a fully erupted M_1 , whereas several of the orangutans with only the deciduous dentition in

occlusion (one as young as 1 year of age, see Table 1, and Fig. 4) have all 7 centers present. The differences seen here may reflect normal variation due to the nature of the sample (cross-sectional with limited numbers of specimens). Although Nissen and Riesen (1949a) give a range of 16–33 months for males and 12–28 months for females for the appearance of the last tarsal ossification center in their sample of nursery-reared chimpanzees, a recent study (Marzke et al., 1996) has suggested greater variability in chimpanzee growth and development than previously reported and has documented differences based on rearing status and environment.

The range of skeletal growth variability is largely undocumented for the great apes. Studies on humans have established relatively wider variability in carpal and tarsal development (Garn et al., 1967; Pyle and Sontag, 1943; Roche, 1992) than in the other secondary ossification centers. In contrast to the evidence from humans, Nissen and Riesen (1949a) have suggested that the onset age of the carpals and tarsals in the chimpanzee is only slightly more variable than that of the other epiphyses. If true, this would render them more useful indicators of age in the chimpanzee. However, the present study has indicated rather wide ranges in the number of tarsal ossification centers present at birth (see discussion above). Much more research is needed with much larger samples of both captive and wild animals to explore this issue and others of great ape development. Presently, the teeth remain much more reliable indicators of age than the skeleton due to their greater resistance to a variety of environmental factors (Roche, 1992).

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